A MULTIVARIATE MORPHOMETRIC STUDY OF THE ASTER GENUS *SERICOCARPUS* (ASTERACEAE: ASTEREAE)

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ABSTRACT

Sericocarpus is a genus of five species of white-rayed asters native to North America. Three species are found in eastern North America (*S. asteroides, S. tortifolius, S. linifolius*) and two are found in western North America (*S. oregonensis, S. rigidus*). *Sericocarpus oregonensis* has been divided into two subspecies based on pubescence and geography (subsp. *californicus* and subsp. *oregonensis*). Over 2300 herbarium specimens were examined to determine the distribution and morphological ranges of variation in traits of each species. Multivariate morphometric analyses of 111 specimens were undertaken to determine which of the 44 vegetative and 19 floral characteristics examined were diagnostic for the species and which species were most similar. The results of cluster and discriminant analyses indicated that all five species were distinct. The species were distinguished on the basis of stem, leaf and floral traits and to a lesser degree on geographic distribution and habitat data. In order to explore the validity of the division of *S. oregonensis* into two infraspecific taxa, stem and leaf pubescence traits were examined on 125 specimens of *S. oregonensis*. The results indicated that *S. oregonensis* can be divided into two subspecies based on pubescence and geography. The statistical results and morphometric measurements were used to construct comprehensive descriptions and an identification key to all taxa of *Sericocarpus*. The pappus was found to be triple or rarely quadruple in all species.

RESUMEN

Sericocarpus es un género norteamericano con cinco especies que tienen los radios blancos. Tres especies se encuentran en el Este (*S. asteroides, S. tortifolius, S. linifolius*) y dos en el Oeste (*S. oregonensis, S. rigidus*). *Sericocarpus oregonensis* ha sido dividido en dos subespecies basadas en la pubescencia y la geografía (subsp. *californicus* y subsp. *oregonensis*). Se han examinado más de 2300 especimenes de herbario para determinar la distribución y los rangos morfológicos de variación en caracteres de todas las especies. Se realizó un análisis morfométrico multivariante de 111 especimenes para determinar cuales de los 44 caracteres vegetativos y 19 florales examinados eran diagnósticos para las especies y que especies eran las más semejantes. Los resultados de los análisis discriminantes y de agrupamiento indican que las cinco especies son diferentes. Las especies se diferencian por caracteres de tallos, hojas y flores, y en menor medida por su distribución geográfica y datos del hábitat. Para comprobar la validez de la división de *S. oregonensis* en dos taxa infraspecíficos, se examinó la pubescencia de tallos y hojas en 125 especimenes de *S. oregonensis*. Los resultados indican que *S. oregonensis* puede dividirse en dos subespecies basadas en la pubescencia y la geografía. Los resultados estadísticos y las medidas morfométricas se usaron para realizar descripciones

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SIDA 21(3): 1471–1505. 2005

detalladas y una clave de identificación de todos los taxa de *Sericocarpus*. Se encontró que el vilano era triple o raramente cuádruple en todas las especies.

INTRODUCTION

The genus *Sericocarpus* Nees (Asteraceae: Astereae) includes five species found only in North America according to the most recent reviews of the genus (Nesom 1993, 1994, 2000; Semple & Leonard 2005). Three of the species occur in the eastern United States (*S. asteroides*, *S. tortifolius* and *S. linifolius*) and two occur in the Pacific States of the United States and on southern Vancouver Island in British Columbia, Canada (*S. oregonensis* and *S. rigidus*). The first of these two western species has been subdivided into two subspecies subsp. *oregonensis* and subsp. *californicus*. Nees (1832) first recognized *Sericocarpus* as a genus distinct from *Aster* L. Others such as Gray (1884), Small (1903), Fernald (1950), and Nesom (1993, 1994, 2000) also treated *Sericocarpus* as a distinct genus. However, in the last fifty years, most botanists have followed Cronquist (1955, 1968, 1980; Gleason & Cronquist 1991) in treating *Sericocarpus* as part of the genus *Aster* in the broad traditional sense, including Jones (1980) and Semple and Brouillet (1980a). Semple et al. (1996) retained *Sericocarpus* within *Aster* subg. *Aster* on the basis of similarities in phyllary traits and the results of a restriction fragment length polymophism analysis of chloroplast DNA (Xiang & Semple 1996), but Semple et al. (2002) treated it as a separate genus based on ITS sequence data, which they summarized and on morphological traits. *Sericocarpus* is more closely related to the goldenrod genus *Solidago* than to other North American species of asters, which themselves can no longer be placed in a large traditionally defined genus *Aster*. DNA studies have shown *Aster* in the new sense is restricted to Europe and Asia with one arctic-alpine exception (Noyes & Rieseberg 1999; Brouillet et al. 2001; Semple et al. 2002). Nesom (2000) included *Sericocarpus* in a narrowly defined subtribe Solidagininae O. Hoffmann; this is one branch of the "North American Clade" of the tribe Astereae (Semple at al. 2002).

Sericocarpus linifolius (L.) B.S.P. is the nomenclatural type of the genus. It has been treated as *Conyza linifolia* L., *Aster linifolius* L. and *Aster solidagineus* Michx., the latter name reflecting similarities to the grass-leaved goldenrods of the genus *Euthamia*, which at the time was erroneously included in *Solidago*. *Sericocarpus linifolius* lacks the prominent basal leaves and dentate leaf margins of *S. asteroides*. Its leaves are linear-oblong to linear-oblanceolate all along the length of the stem. *Sericocarpus linifolius* has the smallest heads in the genus.

Sericocarpus asteroides (L.) B.S.P. has been treated in the past as *Conyza asteroides* L., *Aster asteroides* (L.) MacMillan, *Aster conyzoides* Willd., and *Aster paternus* Cronq. Although other species may exhibit basal leaves, *S. asteroides* has distinctive, serrate, spatulate basal leaves and is the only species to have basal leaves usually present at the time of flowering. The lower stem leaves, also dentate, become progressively more narrowly ovate near the top of the stem.

Sericocarpus tortifolius (Michx.) Nees also has been known, at one time or another, as *Aster tortifolius* Michx., *Aster bifoliatus* (Walt.) Ahles, *Conyza bifoliatus* Walt., and *Sericocarpus bifoliatus* (Walt.) Porter. Its non-dentate leaves are smaller and more oblanceolate than the other four species. Its leaves and stem are the most densely pubescent in the genus. Of the three eastern species, *S. tortifolius* has the smallest range, which extends from southern Florida northeast to North Carolina and west to southern Mississippi.

Sericocarpus linifolius and *S. asteroides* have similar ranges. Both are found along most of the eastern seaboard from New Hampshire down to South Carolina, but they never extend down to southern Georgia or Florida. *Sericocarpus linifolius* occurs a little further west than *S. asteroides* generally does, occurring in western Tennessee and Kentucky. *Sericocarpus linifolius* can also be found in a small area in southeastern Indiana, while *S. asteroides* generally does not extend beyond central Ohio in the north except for a few isolated collections in southern Wisconsin, southwestern Michigan and northwestern Indiana. These latter may be chance adventives.

Sericocarpus oregonensis Nutt. has been treated in the past as *Aster oregonensis* (Nutt.) Cronq., *Sericocarpus californicus* Durand, and *Sericocarpus rigidus* Lindl. in Hook. var. *californicus* (Durand) Blake. The lower leaves of *S. oregonensis* are distinctly reticulate-veined and the heads are usually found in several to many separate clusters. Ferris (1958) divided *Sericocarpus oregonensis* into two taxa: subsp. *californicus* (Durand) Ferris and subsp. *oregonensis*. In the same year, Keck (1958) also recognized two subspecies but treated them in *Aster oregonensis*, as did Allen (1993). In contrast, Nesom (1993) recognized two varieties in the species: *Sericocarpus oregonensis* Nutt. var. *oregonensis* and *Sericocarpus oregonensis* Nutt. var. *californicus* (Durand) Nesom. Nesom (1993) described var. *oregonensis* as having scabrous-puberulent leaves, while var. *californicus* had densely hirsute or pilose leaves (Nesom 1993). *Sericocarpus oregonensis* subsp. *californicus* can be found in the Sierra Nevada range area of eastern California, while subsp. *oregonensis* extends from northern California to western Washington along the Coastal/Cascade ranges.

Sericocarpus rigidus Lindl.in Hook. has a number of nomenclatural synonyms, including *Aster curtus* Cronq. and *Sericocarpus rigidus* Lindley in Hook. var. *laevicaulis* Nutt. It is by far the rarest of the five species of genus. *Sericocarpus rigidus* is similar in appearance to *S. oregonensis* but is smaller in stature, being 1–3 dm tall as opposed to 4–12 dm tall. Furthermore, *S. rigidus* lacks the reticulate-veined lower leaf surfaces of *S. oregonensis*. The heads are usually found in a single cluster with typically 1–3 ray florets as compared to 4–7 in the case of *S. oregonensis*. *Sericocapus rigidus* is found in two isolated pockets, one in western Oregon and the second extending from western Washington at the south end of Puget Sound to the southern tip of Vancouver Island.

In 1990, *Sericocarpus rigidus* was included on the United States Fish and

Wildlife Service's "Endangered and Threatened Wildlife and Plants List" in the Federal Register (Clampitt 1993). In 1996, the Committee on the Status of Endangered Wildlife in Canada (COSEWIC) assigned to *Aster curtus* (Cronq.) the status of "threatened" and revised the listing to *Sericocarpus rigidus* in 2000. COSEWIC describes threatened species as those "likely to become endangered if limiting factors are not reversed" (Douglas & Illingworth 1996). In the case of *S. rigidus*, the principal "limiting factor" is habitat destruction. Most populations are also threatened by competition from aggressive exotic species, such as *Cytisus scoparius*. Fire suppression has also favored the expansion of native species, such as *Symphoricarpos albus*. The proliferation of this shrub is crowding out *S. rigidus* from its natural habitat (Douglas & Illingworth 1996).

All chromosome number reports in *Sericocarpus* are diploid. In total, 44 chromosome count reports of $2n = 9_{II}$ or $2n = 18$ have been published: 14 for *S. asteroides*, five for *S. linifolius*, 14 for *S. oregonensis*, and 11 for *S. tortifolius*. (Huziwara 1965; Anderson et al. 1974; Pinkava & Keil 1977; Semple & Brouillet 1980b; Hill 1983; Semple et al. 1983; Jones & Smogor 1984; Semple 1985; Semple et al. 1989, 1992, 1993; 2001; Semple & Cook 2004). No count is known for *S. rigidus*. Polyploidy is unknown in the genus and thus is not a factor influencing morphology.

The goal of this study was twofold. First, a multivariate morphometric analysis of the genus had never been undertaken before. Second, detailed descriptions were needed to be prepare the treatment of the genus for Flora North America Project (Semple & Leonard 2005). The names of taxa used in this paper are those accepted at the conclusion of this study.

MATERIAL AND METHODS

Over 2300 herbarium specimens of *Sericocarpus* were examined; These were borrowed from or examined at BRIT, CAS, DAO, GH, LINN, MO, NY, ORE, OSC, UC, UVIC, WAT, WILLU and WTU (Holmgren et al. 1990). Of these, 111 specimens were selected for multivariate analyses based on their completeness and developmental stage. Forty-four vegetative and 19 floral characteristics were measured for each of the selected specimens. Some traits such as lower stem leaf features were not available for scoring on all specimens (Table 1). When possible, all traits were measured in replicates of five. Character measurements were then averaged and these averages were used in subsequent statistical analyses. Ray and disk achene pubescence was scored on a scale of 1–5 with 5 representing the highest degree of pubescence. Shape of the leaf apex and base were scored on a scale of 1–10 using a reference card developed in the laboratory.

Each specimen was assigned to an *a priori* group based on geography and morphological characteristics, which were determined through observations and a review of the literature (Nesom 1993). The exclusion of *a priori* traits from discriminant analyses avoided the introduction of circular logic and bias into

the statistical analyses. When a pair of traits highly correlated with one another (Pearson's correlation coefficient ($R = |0.7|$) one of the pair was excluded from further analyses. Highly correlated traits were excluded because two traits showing high correlation could indicate that the phenotype of those two traits resulted from the regulation of a single gene, in which cases, including both traits would be redundant.

Analysis of pubescence variation in the two subspecies of *Sericocarpus oregonensis* (subsp. *oregonensis* and subsp. *californicus*) was assessed by measuring the number of hairs per mm^2 for each of the traits listed in Table 2.

All clustering and discriminant analyses were performed using either SYSTAT 10.0 (SPSS Inc. 2000) or SAS ver. 8.0 (SAS Institute Inc. 1999) software packages. UPGMA cluster analyses using average linkage on squared Euclidian distances were performed in order to determine the relative similarities among the 111 specimens. The cluster analysis used standardized data and all measured traits, with the exception of basal leaf traits, which were only present on *Sericocarpus asteroides* at the time of flowering.

For the canonical analyses, characters not used to define *a priori* group were selected based on the results of a stepwise discriminant analysis, which determines which traits best separate the *a priori* groups. Only nine traits with the highest F-values were then used in a classificatory discriminant analysis because only nine specimens of *Sericocarpus rigidus* were included.

A classificatory discriminant analysis assigns specimens *a posteriori* to groups using the set of characteristics chosen in the stepwise discriminant analysis. The classificatory analysis also includes a test for equality between group centroids (Wilk's lambda, Pillai's Trace and Lawley-Hotelling trace). Geisser assignment probabilities and correct classification rates were also determined. These assess the reliability of the *a posteriori* classification of the specimens relative to the *a priori* groupings and the strengths of alternative placements of the specimens.

Canonical discriminant analysis is a dimensional-reduction technique used to help visualize the results of the discriminant analyses. The number of canonical scores that can be used is one less then the number of *a priori* groups up to three. Canonical score plots were rotated to determine if a single perspective would suffice to illustrate group separation. Two dimensional plots of combinations of canonical scores were also plotted and those that best revealed group separation were selected.

Digital photomicrographs of cyselae were taken using a Nikon CoolPix 990 camera manually held against the ocular lens of either the dissecting or compound microscope. Pictures were taken of specimens under the compound light microscope with either below stage or above stage lighting. Final digital illustrations were made using CorelDraw 12® from digital images edited with Corel PhotoPaint12® (Corel Corp.). In some illustrations the contrast was manipulated

TABLE 1. Traits measured for the morphometric analysis of *Sericocarpus*.

STLNG	Stem length (mm)
STHRLO	Number of hairs on the lower stem per mm^2
STHRMD	Number of hairs on the mid stem per mm^2
STHRUP	Number of hairs on the upper stem per mm^2
BLHRSU	Number of hairs on the basal leaf surface per mm^2
BLHRMR	Number of hairs on the basal leaf margins per mm^2
BLHRVN	Number of hairs on the basal leaf vein per mm^2
BLLENG	Basal leaf length (mm)
BLWID	Basal leaf width (mm)
BLWTIP	Basal leaf measured from the widest point to the tip (mm)
BLAPX	Basal leaf shape at its apex (1–10)
BLBASE	Basal leaf shape at its base (1–10)
BLDENT	Basal leaf dentation—number of serration on the leaf margin
BLBEAD	Number of resin beads on the basal leaf per mm^2
LLHRSU	Number of hairs on the lower leaf surface per mm^2
LLHRMG	Number of hairs on the lower leaf margin per mm^2
LLHRVN	Number of hairs on the lower leaf vein per mm^2
LLLENG	Lower leaf length (mm)
LLWIDE	Lower leaf width (mm)
LLWTIP	Lower leaf measured from the widest point to the tip (mm)
LLAPX	Lower leaf shape at its apex (1–10)
LLBASE	Lower leaf shape at its base (1–10)
LLDENT	Lower leaf dentation—number of serration on the leaf margin
LLBEAD	Number of resin beads on the lower leaf per mm^2
MLHRSU	Number of hairs on the mid leaf surface per mm^2
MLHRMG	Number of hairs on the mid leaf margin per mm^2
MLHRVN	Number of hairs on the mid leaf vein per mm^2
MLLENG	Mid leaf length (mm)
MLWIDE	Mid leaf width (mm)
MLWTIP	Mid leaf measured from the widest point to the tip (mm)
MLAPX	Mid leaf shape at its apex (1–10)
MLBASE	Mid leaf shape at its base (1–10)
MLDENT	Mid leaf dentation—number of serrations on the leaf margin
MLBEAD	Number of resin beads on the mid leaf surface per mm^2
ULHRSU	Number of hairs on the upper leaf surface per mm^2
ULHRMG	Number of hairs on the upper leaf margin per mm^2
ULHRVN	Number of hairs on the upper leaf vein per mm^2
ULLENG	Upper leaf length (mm)
ULWIDE	Upper leaf width (mm)
ULWTIP	Upper leaf measured from the widest point to the tip (mm)
ULAPX	Upper leaf shape at its apex (1–10)
ULBASE	Upper leaf shape at its base (1–10)
ULDENT	Upper leaf dentation—number of serrations on the leaf margin
ULBEAD	Number of resin beads on the upper leaf surface per mm^2
NOINFL	Number of heads on lateral branch
HDHGT	Head height (mm)
HDWIDE	Head width (mm)
OUTPHY	Outer phyliary length (mm)
TWOPHY	Second layer phyllary length (mm)
THRPHY	Third layer phyllary length (mm)
INPHY	Inner phyllary length (mm)
RAYFLR	Number of ray florets per head
RSTRLNG	Ray strap length (mm)
RCORTB	Ray corolla tube length—measured from base to beginning of strap (mm)
RACHLNG	Ray cypsela body length (mm)
RPAPLNG	Ray cypsela pappus length (mm)
RPBSC	Ray cypsela pubescence (0–5)
DISFLOR	Number of disc florets per head
DCORTB	Disc corolla tube length (mm)
DACHLNG	Disc cypsela body length (mm)
DPAPLNG	Disc cypsela pappus length (mm)
DPBSC	Disc cypsela pubescence (0–5)
DCORLB	Disc corolla lobe length (mm)

TABLE 2. Traits measured for the pubescence analysis of *Sericocarpus oregonensis*; all counts are given in numbers of hairs/mm^2.

STHRLO	Number of hairs on lower stem.	MLHRSU	Number of hairs on mid leaf surface.
STHRMD	Number of hairs on mid stem.	MLHRVN	Number of hairs on mid leaf vein.
STHRUP	Number of hairs on upper stem.	MLHRMG	Number of hairs on mid margin.
LLHRSU	Number of hairs on lower leaf surface.	ULHRSU	Number of hairs on upper leaf surface.
LLHRVN	Number of hairs on lower leaf vein.	ULHRVN	Number of hairs on upper leaf vein.
LLHRMG	Number of hairs on lower leaf margin.	ULHRMG	Number of hairs on upper leaf margin.

to increase the difference between pappus bristles and background for illustrative purposes.

RESULTS

Cluster analyses

Standardized data for 53 characters (Table 1) were included in an UPGMA cluster analysis. Traits not included were those for which data was not available for all specimens, e.g. stem height and lower leaf traits. Results indicate separation into four main branches (Fig. 1; A–D) and two small basal clusters. The three eastern species clustered into three groups corresponding to the species with only three exceptions. Branch A included all the specimens of *Sericocarpus tortifolius* and no other taxa. Branch B included all but one of the *S. linifolius* specimens, with no inclusion of specimens of any other taxa. The single exception was a *S. linifolius* specimen (lin32), which occurred on a more basal branch along with one *S. asteroides* specimen (ast26). Branch C included all but two of the measured *S. asteroides* specimens, as well as two small *S. oregonensis* specimens (cal23 & cal19). Of the two *S. asteroides* specimens not clustered within Branch C, one specimen clustered with one *S. linifolius* specimen. The other *S. asteroides* specimen (ast92) occurred by itself on the basal branch of the dendrogram; it was a robust individual.

Branch D consisted of only members of the two western species *Sericocarpus oregonensis* and *S. rigidus*. The branch was subdivided into three clusters (a, b and c). Branch c included all nine *S. rigidus* specimens as well as two smaller *S. oregonensis* subsp. *oregonensis* specimens (oreg101 & oreg107). Branches a and b were composed entirely of *S. oregonensis* specimens with both clusters including specimens from the Sierras (subsp. *californicus*) and from the Coastal and Cascade Mts. (subsp. *oregonensis*). Six of the eight specimens in cluster a belonged to subsp. *californicus*. Four of the six specimens in cluster b belonged to subsp. *oregonensis*. The two specimens of subsp. *californicus* in cluster b had pubescence values at the lower end of the ranges of the traits for the subspecies.

A cluster analysis was performed on a matrix of 12 stem and leaf pubescence traits scored on 107 specimens of *S. oregonensis*. Specimens of the two subspecies were intermixed and did not form two distinct cluster groups corresponding to the geographically based subspecies.

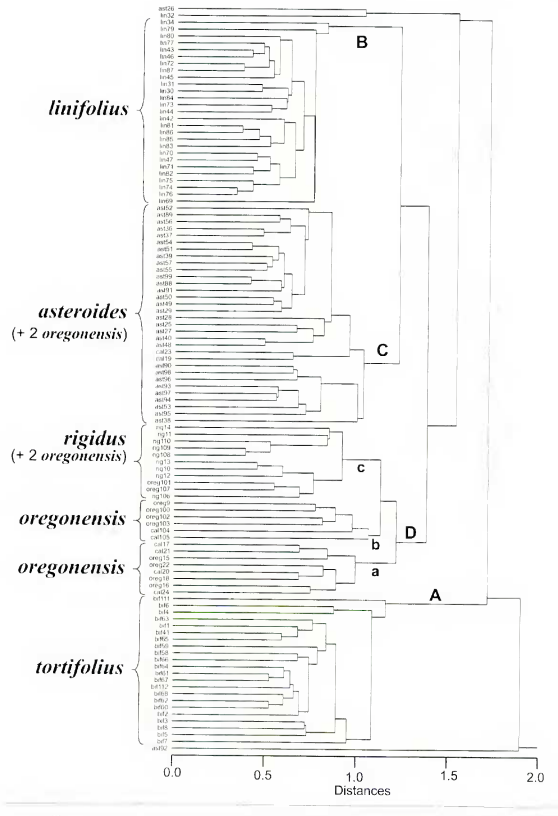

Fig. 1. UPGMA cluster analysis based on all characters. Branches indicated by letters are discussed in the text.

Discriminant Analyses

A canonical discriminant analysis was carried out on 107 specimens of *Sericocarpus*. *A priori* group membership was determined using the characteristics listed in Table 3. Leaf length, width and pubescence, as well as stem pubescence were diagnostic traits used in the assignment of all specimens into *a priori* groups. Specimens were assigned to groups in part on the basis of geographic distribution. In the literature, five species level groups have been widely accepted (e.g., Nesom 1993). Examination of more than 2300 specimens indicated that five species groups were recognizable using key characters from the literature. Three *a priori* groups included only specimens from the eastern United States. Specimens assigned *a priori* to the *S. tortifolius* group were the most pubescent, had obovate upper stem leaves and all came from the southeastern United States. Specimens assigned *a priori* to the *S. linifolius* group were glabrous for all traits listed in Table 3, had narrowly elliptic, lanceolate or linear leaves, and all came from the eastern United States. Specimens of the *S. linifolius* group also had the longest mid and upper stem leaves. Specimens assigned *a priori* to the *S. asteroides* group were from the eastern United States and had basal rosette and lower stem leaves that were petiolate and obovate to oblanceolate and usually serrate; upper stem leaves were reduced, becoming sessile and ovate to lanceolate. The widest lower and mid stem leaves were observed on specimens of *S. asteroides*.

Western North American specimens were assigned *a priori* to *S. oregonensis* and *S. rigidus*. Specimens with one or two ray florets with short straps were assigned *a priori* to the *S. rigidus* group; these came from the south end of Vancouver Island in British Columbia and western Washington and Oregon. Western specimens with at least three ray florets with longer, broader straps were assigned *a priori* to the *S. oregonensis* group, which was not subdivided into subspecies groups for the species level analysis. On average, *S. oregonensis* specimens tended to have the widest upper stem leaves.

A stepwise discriminant analysis was used to select traits to be included in the discriminant functions used in further analyses. The means, standard deviations, ranges, and minimum and maximum values of all characters analyzed are presented in Table 4. The nine characters selected and used in further analyses are indicated by asterisks. The stepwise discriminant analysis selected twelve traits as having some value in discriminating groups. Of these, the three with the lowest F-values (HDHGT, RCORTB, DISFLOR) were discarded in order that the number of traits used in the classificatory discriminant analysis not exceed the number of specimens in the smallest *a priori* group; nine suitable specimens of *S. rigidus* were included. Other traits scored were rejected from further analysis because they correlated highly with traits included in the stepwise discriminant analysis.

TABLE 3. Characteristics used to make *a priori* group assignments to five species level groups in *Sericocarpus*; means, ± standard deviations, (ranges) and minimum / maximum; all lengths and widths are given in mm and all pubescence counts are given in numbers of hairs/mm².

Character	*S. asteroides*	*S. tortifolius*	*S. linifolius*	*S. oregonensis*	*S. rigidus*
STHRLO	2.63 ± 2.37 (0.26–4.99) 0 / 9	34.45 ± 12.85 (21.61–47.30) 0 / 55	0.00 ± 0.00 (0.00–0.00) 0 / 0	8.44 ± 6.46 (1.99–14.90) 0 / 23	1.78 ± 2.39 (0.00–4.16) 0 / 6
STHRMD	6.00 ± 3.45 (2.55–9.45) 0 / 15	39.73 ± 6.85 (32.88–46.57) 30 / 55	0.00 ± 0.00 (0.00–0.00)	11.22 ± 4.76 (6.46–15.98) 3 / 18	2.37 ± 4.39 (0.00–7.05) 0 / 13
STHRUP	10.94 ± 5.48 (5.45–16.42) 0 / 25	42.41 ± 9.40 (33.01–51.81) 25 / 59	0.00 ± 0.00 (0.00–0.00) 0 / 0	11.28 ± 5.14 (6.14–16.42) 2 / 20	8.11 ± 8.74 (0.00–16.85) 0 / 25
LLHRSU	2.48 ± 2.10 (0.37–4.58) 0 / 7	22.43 ± 5.56 (16.88–27.99) 14 / 36.67	0.00 ± 0.00 (0.00–0.00) 0 / 0	8.36 ± 3.76 (4.59–12.12) 0 / 13	1.10 ± 1.93 (0.00–3.03) 0 / 4.67
LLLENG	60.03 ± 22.08 (37.95–82.10) 29.70 / 106.25	26.22 ± 5.71 (20.51–31.93) 15 / 38	50.39 ± 12.26 (38.13–62.64) 25.13 / 75.67	57.60 ± 16.82 (40.78–74.42) 39.60 / 97.75	38.95 ± 11.19 (27.77–50.14) 24.83 / 56.50
LLWIDE	16.26 ± 5.55 (10.71–21.81) 7 / 28.25	9.33 ± 2.52 (6.81–11.85) 5.25 / 14.00	5.86 ± 1.52 (4.34–7.38) 3 / 9.50	10.40 ± 2.76 (7.63–13.16) 7 / 16.13	6.91 ± 1.04 (5.86–7.95) 5.50 / 8.92
MLHRSU	2.37 ± 2.36 (0.01–4.73) 0 / 7.00	26.85 ± 4.93 (21.92–31.78) 18 / 41.33	0.00 ± 0.00 (0.00–0.00) 0 / 0	11.52 ± 6.01 (5.51–17.52) 0 / 21.67	2.11 ± 3.06 (0.00–5.18) 0 / 8.80
MLLENG	37.22 ± 11.80 (25.42–49.02) 16.17 / 57.90	21.90 ± 5.69 (16.21–27.59) 12.75 / 34.60	41.53 ± 6.60 (34.93–48.14) 27.10 / 52.40	43.61 ± 12.42 (31.19–56.03) 29.50 / 80.25	33.50 ± 9.53 (23.97–43.02) 20.88 / 46.50
MLWIDE	11.15 ± 3.52 (7.63–14.67) 6.50 / 20.75	8.52 ± 2.27 (6.25–10.79) 5.20 / 14.00	3.87 ± 0.74 (3.13–4.61) 2.40 / 6.10	10.33 ± 2.78 (7.55–13.11) 6.44 / 16.27	6.91 ± 1.43 (5.48–8.34) 4.97 / 9.25
ULHRSU	1.94 ± 2.13 (0.00 ± 4.07) 0 / 9.00	30.74 ± 7.97 (22.77–38.72) 18.20 / 54.33	0.00 ± 0.00 (0.00–0.00) 0 / 0	14.96 ± 9.37 (5.60–24.33) 3 / 34	1.98 ± 2.55 (0.00–4.53) 0 / 6.60
ULLENG	21.27 ± 6.50 (14.78–27.77) 11.00 / 44.83	14.37 ± 2.89 (11.49–17.26) 9.70 / 21.60	24.73 ± 5.42 (19.31–30.16) 13.67 / 36.90	22.97 ± 7.50 (15.48–30.47) 12.25 / 42.75	22.00 ± 6.71 (15.29–28.72) 12.67 / 33.50
ULWIDE	6.16 ± 1.92 (4.24–8.07) 3.75 / 11.00	5.93 ± 1.32 (4.61–7.25) 3.45 / 8.20	2.81 ± 0.61 (2.20–3.42) 1.85 / 4.10	6.41 ± 1.63 (4.78–8.04) 3.50 / 10.00	4.98 ± 1.16 (3.82–6.14) 3.70 / 7.38
RSTRLNG	4.30 ± 0.84 (3.46–5.15) 2.48 / 6.03	4.80 ± 0.92 (3.88–5.72) 3.38 / 6.35	6.00 ± 1.47 (4.53–7.47) 4.19 / 10.50	4.46 ± 0.76 (3.70–5.23) 3.10 / 5.59	2.10 ± 0.55 (1.55–2.64) 1.56 / 3.00
RAYFLR	5.06 ± 0.99 (4.07–6.05) 3.20 / 7.60	3.90 ± 0.85 (3.05–4.76) 2.00 / 5.40	3.80 ± 0.98 (2.82–4.79) 2.80 / 6.40	4.08 ± 1.22 (2.86–5.29) 2.00 / 5.80	1.45 ± 0.54 (0.91–1.99) 0.75 / 2.33

TABLE 4. Characteristics included in a stepwise discriminant analysis of five *a priori* species groups of *Sericocarpus*; means ± standard deviations, (ranges), and minimum and maximum values; all lengths are given in mm and all pubescence counts are given in numbers of hairs/mm²; characteristics are shown in order of decreasing F-values; traits selected by the analysis are indicated by and asterisk*.

Character	*S. asteroides*	*S. tortifolius*	*S. linifolius*	*S. oregonensis*	*S. rigidus*
THRPHY*	5.70 ± 0.72 (4.98–6.43) 4.17 / 7.14	4.43 ± 0.59 (3.85–5.02) 3.61 / 6.07	4.62 ± 0.41 (4.21–5.04) 3.84 / 5.45	6.38 ± 0.64 (5.74–7.01) 4.69 / 7.15	7.26 ± 0.87 (6.39–8.13) 6.13 / 8.57
MLHRVN*	6.63 ± 3.12 (3.52–9.75) 0 / 12.00	14.29 ± 3.42 (10.87–17.71) 10.20 / 22.00	0.00 ± 0.00 (0.00–0.00) 0 / 0	7.67 ± 3.51 (4.16–11.17) 2.00 / 15.00	3.37 ± 2.56 (0.81–5.93) 0 / 6.80
DCORLB*	0.94 ± 0.18 (0.76–1.12) 0.6 / 1.5	1.37 ± 0.23 (1.15–1.60) 1.05 / 1.78	1.45 ± 0.23 (1.22–1.68) 1.05 / 1.94	1.21 ± 0.16 (1.05–1.38) 1.00 / 1.66	0.83 ± 0.10 (0.73–0.93) 0.63 / 0.96
ULHRMG*	5.68 ± 1.76 (3.92–7.44) 2.67 / 8.60	13.20 ± 3.08 (10.12–16.29) 8.80 / 22.00	3.85 ± 1.28 (2.57–5.13) 1.33 / 7.20	4.57 ± 5.32 (0.00–9.88) 0 / 12.40	8.77 ± 1.39 (7.37–10.16) 7.20 / 11.50
DCORTB*	3.70 ± 0.33 (3.37–4.04) 3.22 / 4.35	4.82 ± 0.63 (4.19–5.46) 3.84 / 5.95	3.10 ± 0.38 (2.72–3.47) 2.25 / 3.75	4.59 ± 0.46 (4.12–5.05) 3.39 / 5.15	5.09 ± 0.52 (4.58–5.61) 4.44 / 6.23
RACHLNG*	1.19 ± 0.22 (0.98–1.41) 0.80 / 1.84	1.48 ± 0.29 (1.20–1.77) 1.14 / 2.35	0.97 ± 0.11 (0.86–1.08) 0.73 / 1.22	2.06 ± 0.56 (1.5–2.62) 1.27 / 3.32	1.58 ± 0.36 (1.23–1.94) 1.25 / 2.19
MLWTIP*	17.13 ± 6.29 (10.84–23.41) 7.38 / 30.25	8.46 ± 4.23 (4.23–12.69) 4.40 / 24.50	18.59 ± 3.62 (14.96–22.21) 13.30 / 27.00	20.02 ± 6.73 (13.29–26.75) 11.50 / 33.30	12.40 ± 3.35 (9.05–15.75) 8.06 / 18.50
HEWIDE*	4.44 ± 0.70 (3.75–5.14) 3.08 / 6.00	5.24 ± 1.49 (3.76–6.73) 3.50 / 10.53	3.19 ± 0.67 (2.51–3.86) 2.26 / 4.82	5.79 ± 0.84 (4.95–6.63) 4.44 / 7.19	5.55 ± 0.86 (4.68–6.41) 4.10 / 6.54
ULHRVN*	6.03 ± 2.70 (3.34 8.73) 0 / 12.33	12.62 ± 7.33 (5.29–19.96) 0 / 20.80	0.00 ± 0.00 (0.00–0.00) 0 / 0	8.63 ± 3.18 (5.45–11.81) 3.00 / 16.50	3.53 ± 2.72 (0.81–6.25) 0.20 / 7.40
RCORTB	3.08 ± 0.45 (2.63–3.53) 2.36 / 4.23	3.40 ± 0.39 (3.01–3.80) 2.67 / 4.19	3.08 ± 0.42 (2.66–3.51) 2.35 / 3.96	3.15 ± 0.33 (2.82–3.49) 2.55 / 3.71	3.07 ± 0.46 (2.61–3.53) 2.50 / 3.88
HEHGT	8.24 ± 0.84 (7.4–9.09) 7.03 / 10.44	10.63 ± 0.96 (9.67–11.58) 9.25 / 13.78	6.92 ± 0.72 (6.20–7.65) 5.63 / 8.38	10.17 ± 1.16 (9.02 ± 11.33) 7.89 / 12.13	10.53 ± 1.01 (9.52–11.54) 9.35 / 12.37
DISFLOR	13.51 ± 2.59 (10.92–16.10) 9.60 / 19.20	8.65 ± 1.21 (7.45–9.86) 6.40 / 10.80	8.61 ± 2.32 (6.28–10.93) 5.20 / 14.60	13.41 ± 3.08 (10.32–16.49) 9.00 / 19.25	13.03 ± 2.43 (10.60–15.46) 9.5 / 16.8
OUTPHY	3.28 ± 0.44 (2.84–3.72) 2.36 / 4.20	2.24 ± 0.34 (1.9–2.58) 1.76 / 3.12	2.96 ± 0.27 (2.69–3.23) 2.40 / 3.49	3.92 ± 0.49 (3.43–4.42) 2.76 / 4.57	4.21 ± 0.73 (3.48–4.93) 3.14 / 5.29
ULWTIP	10.75 ± 3.64 (7.10–14.39) 5.19 / 19.50	5.35 ± 1.14 (4.22–6.49) 2.42 / 7.50	13.76 ± 2.95 (10.81–16.72) 8.83 / 19.00	11.56 ± 3.85 (7.70–15.41) 5.88 / 20.75	9.23 ± 2.10 (7.13–11.33) 6.95 / 12.30

TABLE 4 continued

Character	*S. asteroides*	*S. tortifolius*	*S. linifolius*	*S. oregonensis*	*S. rigidus*
MLHRMG	5.62 ± 1.72 (3.90–7.34) 3.00 / 8.25	11.93 ± 1.99 (9.94–13.92) 8.67 / 17.33	3.91 ± 1.42 (2.49–5.33) 1.00 / 6.60	4.71 ± 5.88 (0.00–10.59) 0 / 18.50	8.31 ± 1.97 (6.34–10.28) 7.00 / 13.00
NOINFL	3.50 ± 1.28 (2.22–4.78) 2.60 / 5.60	2.98 ± 0.41 (2.57–3.40) 2.40 / 4.00	3.18 ± 1.08 (2.10–4.26) 2.40 / 8.40	3.33 ± 0.36 (2.98–3.69) 2.60 / 4.20	2.87 ± 0.45 (2.42–3.32) 2.20 / 3.40

The Mahalanobis distances between group centroids and the associated F-statistics and their probabilities generated by the classificatory discriminant analysis (Table 5) indicated that all five *a priori* species level groups were strongly supported ($p<0.001$ in all cases). Other tests, i.e. the probabilities for the Wilk's lambda, Pillai's trace, and Lawley-Hotelling trace indicated there were significant differences between group centroids ($p < 0.0001$).

In the classificatory discriminant analysis, specimens was assigned *a posteriori* to five species level groups using the discriminant functions. In the *a posteriori* classification analysis (Table 6), 100% correct classification was made *a posteriori* for specimens assigned *a priori* to *Sericocarpus asteroides*, *S. tortifolius*, and *S. rigidus*. For *S. linifolius*, 96% of the specimens were correctly classified *a posteriori*; one of 28 specimens was assigned to *S. asteroides*. For *S. oregonensis*, 83% were correctly classified; three of 18 specimens were assigned to *S. asteroides*. Overall, 96% of specimens were correctly assigned *a posteriori* to their respective *a priori* groups. In the Jackknifed classification analysis (Table 7), the overall correct *a posteriori* assignment rate was 91%. Again, all specimens were assigned correctly to *S. tortifolius*. The correct classification rates for the other four groups were 90% for *S. asteroides*, 96% for *S. linifolius*, 72% for *S. oregonensis* and 89% for *S. rigidus*.

Plots of the canonical variate scores on the first and second and first and third canonical axes are shown in Fig. 2. Specimens of *S. linifolius* and *S. tortifolius* are separated from the other taxon on the first two axis, while the other three species separate on the first and third axes although with slight overlap toward the center of the distribution of symbols.

Univariate analyses of *S. oregonensis*: subsp. *oregonensis* and subsp. *californicus*

Pubescence traits of 107 specimens of *Sericocarpus oregonensis* were analyzed. The means, standard deviations, ranges (as well as, minimum and maximum values) for stem and leaf pubescence traits measured for subsp. *oregonensis* and subsp. *californicus* are presented in Table 8. Results indicate that subsp. *oregonensis*, which grows in the Coastal/Cascade Mountains region, was less pubescent than subsp. *californicus* found in the Sierra Nevada region of California. Two-sample t tests were run comparing each trait listed in Table 8 by subspecies. Even though the ranges of values of the subspecies overlapped, there

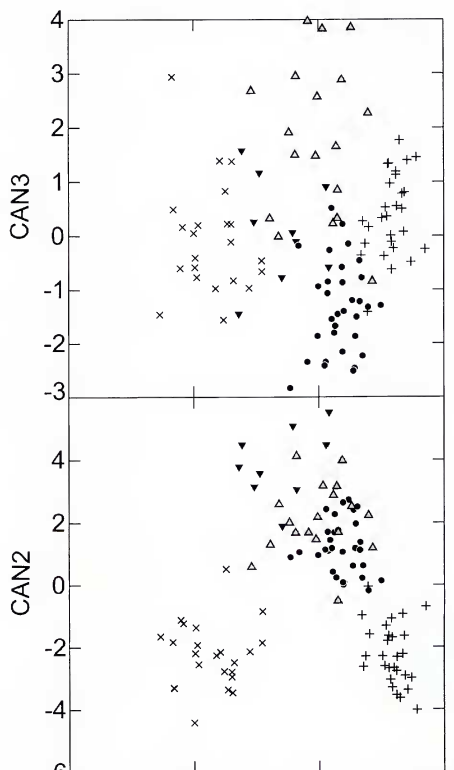

FIG. 2. Plots of the first and second and first and third canonical variates of 107 specimens included in the five taxon canonical analysis of *Sericocarpus*. Key to symbols: *S. asteroides*, **solid dots**; *S. linifolius*, +; *S. oregonensis*, **light shaded triangles**; *S. rigidus*, **inverted black triangles**; and *S. tortifolius*, ×.

TABLE 5. Mahalanobis distances (squared) between group centroids and associated, F-statistics for the five species level groups analysis of *Sericocarpus*; probabilities between groups in all comparisons were < 0.0001.

	a posterori group			
***a priori* group**	**asteroides**	**tortifolius**	**linifolius**	**oregonensis**
S. tortifolius	70.173 91.201			
S. linifolius	20.281 30.077	97.071 122.457		
S. oregonensis	11.865 13.668	59.249 60.062	38.146 42.796	
S. rigidus	18.499 13.114	81.725 53.450	53.885 37.579	20.152 12.381

TABLE 6. Results of an *a posteriori* classificatory discriminant analysis of 107 specimens of *Sericocarpus* using a linear discriminant function.

Group	*a posterori* group					
***a priori* group**	**asteroides**	**tortifolius**	**linifolius**	**oregonensis**	**rigidus**	**N**
asteroides	30 100%	0	0	3 10%	0	30
tortifolius	0	22 100%	0	0	0	22
linifolius	1 4%	0	27 96%	0	0	28
oregonensis	3 17%	0	0	15 83%	0	18
rigidus	1 11%	0	0	0	9 100%	9
TOTALS	34	22	27	16	8	107

was a statistically significant difference ($p=0.00$, $\pm = 0.05$) between the means for every trait.

DISCUSSION

Cluster and discriminant analyses support the division of *Sericocarpus* into five species. *Sericocarpus linifolius* and *S. tortifolius* are the two most distinct species within the genus. *Sericocarpus asteroides*, *S. oregonensis*, and *S. rigidus* are generally more similar to one another with the greatest similarity being between the latter two, which are the western North America species. The similarity between these three latter species is reflected in the inclusion of a few of the *S. oregonensis* specimens within the *S. asteroides* and *S. rigidus* branches in

TABLE 7. Results of an *a posteriori* jackknifed classificatory discriminant analysis of 107 specimens of *Sericocarpus* using a linear discriminant function.

Group	*a posterori* group					
a priori group	asteroides	tortifolius	linifolius	oregonensis	rigidus	N
asteroides	27 90%	0	0	3 10%	0	30
tortifolius	0	22 100%	0	0	0	22
linifolius	1 4%	0	27 96%	0	0	28
oregonensis	5 28%	0	0	13 72%	0	18
rigidus	1 11%	0	0	0	8 89%	9
TOTALS	34	22	27	16	8	107

the cluster analysis, even if such confusion of identity is unlikely due to very different general appearances and provenances. Regardless of the similarity on technical traits as seen in the cluster analysis between *S. asteroides* and the two western species, the 100% correct *a posteriori* classification rate for *S. asteroides* in the classificatory discriminant analysis establishes that it is indeed a distinct species, especially considering the obvious basal rosette trait was not included in the analyses. The technical similarities in traits scored is not reflected in the ease with which *S. asteroides* can be identified in the field.

All of the specimens placed *a posteriori* by the classificatory discriminant analysis into a different group than their *a priori* placements were examined and found to have been correctly placed *a priori* on the basis of the diagnostic traits not included in the analyses. While readily identified as belonging to one of the *a priori* groups, the specimens generally were either stunted or robust compared to other members of the group. Thus, either favorable or unfavorable growing conditions likely influenced others traits that were included in the analyses. The *S. linifolius* specimen not included in Branch B of the cluster diagram (Fig. 1) was also the one misclassified specimen in the classification matrix generated by the classificatory discriminant analysis. This specimen was found to be a very robust plant for the species, therefore explaining its *a posteriori* inclusion into the *S. asteroides* group. There is no doubt that it is specimen of *S. linifolius* based on the *a priori* characteristics excluded from the analyses.

The three misclassified *Sericocarpus oregonensis* specimens were examined, and though some did not always conform to the norm for one trait or another, the initial *a priori* assignments were correct. One of the misclassified *S. oregonensis* specimens (cal23), clustered, along with a second *S. oregonensis*

TABLE 8. Pubescence characteristics measured for the two subspecies of *S. oregonensis*; means ± standard deviations, (ranges), and minimum / maximum values; all pubescence counts are given in numbers of hairs/mm².

Character	subsp. oregonensis *n* = 63	subsp. californicus *n* = 62
STHRLO	9.54 ± 3.88 (5.65–13.42) 1.00 / 18.00	14.07 ± 3.52 (10.55–17.59) 4.00 / 23.00
STHRMD	10.89 ± 4.36 (6.53–15.25) 2.00 / 24.00	14.27 ± 3.20 (11.07–17.47) 7.00 / 22.00
STHRUP	12.03 ± 4.19 (7.84–16.22) 4.00 / 26.00	18.26 ± 4.96 (13.30–23.21) 11.00 / 33.00
LLHRSU	8.57 ± 3.41 (5.16–11.98) 2.00 / 19.33	14.75 ± 4.57 (10.18–19.32) 7.00 / 25.20
LLHRVN	5.16 ± 1.60 (3.56–6.76) 2.00 / 8.60	7.84 ± 1.70 (6.15–9.54) 3.00 / 11.40
LLHRMG	7.57 ± 1.63 (5.94–9.20) 4.67 / 13.40	9.38 ± 1.75 (7.64–11.13) 6.00 / 13.20
MLHRSU	10.00 ± 3.83 (6.17–13.83) 2.00 / 19.00	16.72 ± 4.12 (12.61–20.84) 6.67 / 27.00
MLHRVN	5.52 ± 1.48 (4.04–7.00) 2.75 / 9.60	8.48 ± 2.04 (6.44–10.52) 4.00 / 13.80
MLHRMG	7.54 ± 1.58 (5.96–9.11) 4.75 / 11.40	9.38 ± 1.92 (7.46–11.30) 5.80 / 14.80
ULHRSU	12.32 ± 4.65 (7.67–16.97) 3.67 / 23.80	20.49 ± 4.56 (15.93–25.04) 8.33 / 29.60
ULHRVN	5.90 ± 1.54 (4.36–7.44) 2.67 / 11.00	8.88 ± 1.75 (7.13–10.63) 5.33 / 13.40
ULHRMG	8.00 ± 1.75 (6.24–9.75) 4.00 / 13.60	10.22 ± 1.79 (8.43–12.01) 6.60 / 14.20

specimen, within the *S. asteroides* group. Both of these were smaller, less robust plants. Two *S. oregonensis* specimens clustered within the *S. rigidus*. These specimens were dwarf plants with stem lengths corresponding to the lower end of the range for the species (STLNG = 24 cm and 46.5 cm, respectively, Mean = 62.4 mm). The remaining *S. oregonensis* specimens clustered into two groups. The branch b cluster in Fig. 1 is composed of four individuals of *S. oregonensis* subsp. *oregonensis* and two of *S. oregonensis* subsp. *californicus*. The latter two specimens have low hair counts for the subspecies (ULHRSU = 16.6 hairs/mm^2 and 18.8 hairs/mm^2, respectively; mean = 20.5 hairs/mm^2). The branch a cluster in Fig. 1 is composed of six *S. oregonensis* subsp. *californicus* and two *S. oregonensis* subsp. *oregonensis* specimens. Upon close re-examination of the two *S. oregonensis* subsp. *oregonensis* specimens, no obvious morphological traits which could account for its clustering within branch a were observed.

Of the five *Sericocarpus* species, *S. tortifolius* is the most distinct on scored technical traits. All cases clustered together with no inclusion of specimens from any other species. *Sericocarpus tortifolius* is also the only species to show 100% correct classification rates in both the Classification and Jacknifed matrices. The highest F-value (F = 122.457) and Mahalanobis distance (D = 97.071) occurred between the *S. linifolius* and the *S. tortifolius* group centroids. These results confirm the cluster analysis and canonical analysis results which indicate that of the five species, *S. linifolius* and *S. tortifolius* are the most distinct.

Of the one-hundred and seven specimens assigned *a posteriori* during a classificatory discriminant analysis, only four specimens were misclassified. The average Geiser assignment probabilities were: 0.94 for *S. asteroides*, 1.00 for *S. tortifolius*, 0.97 for *S. linifolius*, 0.82 for *S. oregonensis*, and 0.97 for *S. rigidus*. These high Geiser assignment probabilities indicate that the within-group variances are small in comparison to the between-group variances.

The strong F-values and low probabilities of the Wilk's lambda ($F = 34.863$, $p < 0.001$), Pillai's Trace ($F = 22.640$, $p < 0.001$) and Lawley-Hotelling trace ($F = 48.065$, $p < 0.001$) generated during the classificatory discriminant analysis, all indicate that the probability that all specimens tested are representative of one single group rather than five species groups is extremely small.

Scoring of canonical traits on the first and second axes show strong group separation by *S. tortifolius* and *S. linifolius*. The overlapping of the three remaining species on the first and second axes is resolved when the canonical scores are plotted on the second and third canonical axes. The separation visualized in the canonical analysis is supported by the aforementioned cluster and discriminant analyses.

The division of *S. oregonensis* into two subspecies, subsp. *oregonensis* and subsp. *californicus*, is based on both geographic and morphological traits. Those plants growing in the Coastal/Cascade Mountain ranges of Washington, Oregon and California (subsp. *oregonensis*) are more sparsely pubescent than those

plants growing in the Sierra Nevada region of eastern California (subsp. *californicus*). The ranges for both subspecies overlap in far northern California; however, the means for all measured pubescence traits is consistently smaller in the case of *S. oregonensis* subsp. *oregonensis* specimens. Two-sample t test results indicate that the difference between the means of both subspecies is statistically significant (prob = 0.00, C.I. = 95%). *Sericocarpus oregonensis* is also found in an intermediate geographical region, namely Butte and Shasta counties in California, where both subspecies are found, but can easily be assigned to appropriate subspecies by examining pubescence traits.

In conclusion, based on the results of the multivariate morphometric analyses, and to a lesser extent on geographical data, the aster genus *Sericocarpus* should be divided into five species: *S. asteroides*, *S. tortifolius*, *S. linifolius*, *S. oregonensis*, and *S. rigidus*. Differences in the degree of pubescence and in geographical location within *S. oregonensis*, support the separation of this species into two infraspecific taxa: *Sericocarpus oregonensis* subsp. *oregonensis*, found in the coastal/cascade region of Washington, Oregon, and California is more sparsely pubescent than *S. oregonensis* subsp. *californicus*, which grows in the Sierra Nevada region of California. Subspecies ranks is adopted following Semple (1974) because the two infraspecific taxa have essentially allopatric distributions. For an alternative usage of infraspecific ranks see Turner and Nesom (2000) who presented the argument that subspecies rank should be used as a grouping category only like subgenus, subtribe, etc. We find it useful to continue to use two infraspecific ranks (subspecies and variety) to emphasize geographic features of the taxa.

TAXONOMIC TREATMENT[4]

Sericocarpus Nees, Gen. et sp. Aster. 10, 148. 1832. *Aster* subg. *Sericocarpus* (Nees) A.G. Jones Brittonia 32: 238. 1980. *Aster* sect. *Sericocarpus* (Nees) Semple, Phytologia 58:429. 1985. LECTOTYPE [Britt. in Britt. & Brown 1913]: *Sericocarpus solidagineus* (Michx.) Nees = *Sericocarpus linifolius* (L.) B.S.P.

Aster sect. *Serratifolii* Loudon, Hort Brit. 347. 1830. "Leaves lanceolate and ovate, lower ones serrate" LECTOTYPE [Sundberg & Jones 1987]: *Aster conyzoides* Willd. = *Sericocarpus linifolius* (L.) B.S.P.

Perennial herbs from rhizomatous to stout, branching, woody caudex. Stem erect, glabrate to pubescent, (15–)32–48–62(–117) cm. Basal leaves usually absent at time of flowering, puberulent, (2–)4–8–11(–15) cm long, serrate near apex, spatulate to petiolate, reticulate veined. Stem leaves linear to (ob)ovate, sessile, acuminate to acute, sometime slightly cuspidate (1–)2–3–5(–11) cm long, (0.1–) 0.4–0.8–1(–3) cm wide, reticulate veined, glabrate to moderately hispidulous or hispidulous-pilose, hairs 0.05–0.5 mm long, longest hairs sometimes twisted,

[4]All measurements in the taxonomic treatment are given in the following format: (minimum)–minus the standard deviation–**mean**–plus the standard deviation–(maximum).

usually sparsely to moderately finely glandular punctuate, the stipitate-glands recessed, sometimes resinous, margins ciliate, serrate becoming entire or entire, upper leaves decreasing in size upward. Capitulescence corymbiform to broadly corymbiform, sometimes compact; heads 2–5 per branch; bracts, ciliate, glabrate to pubescent, broadly lanceolate to narrowly ovate. Involucre (3.8–)5.0–6.0–7.0(–8.6) mm high at anthesis, (2.3–)3.8–4.8–5.9(–10.5) mm wide; phyllaries in 3–5 imbricate series, ciliate, glabrate to pubescent, base narrowly to widely oblong, tip narrowly to broadly acute, outer series (1.8–)2.5–3.3–4.1(–5.3) mm long, mid series (2.7–)3.5–4.4–5.2(–6.5) mm long, inner series more linear and less chlorophyllous, margins ciliate, dark green zone at the apex, thumb-nail shaped. Ray florets 1–6, strap (1.6–)2.9–4.3–5.8(–10.5) mm long, corolla tube (2.4–)3.0–3.2–3.3(–4.2) mm long, cypselae strigose to densely strigose, (0.7–)1.0–1.5–1.9(–3.3) mm long at anthesis, increasing twofold by maturity,pappus, triple or rarely quadruple: secondary outer series of very few linear scales, 0.1–1mm long; middle and inner series of barbellate bristles, secondary inner series of mid length tapering bristles, 35–70% the length of the primary inner series; primary outer series of tapering bristles 80–95% the length of the primary inner bristles; primary inner series bristles strongly clavate, (3.5–)4.3–5.2–6.1(–7.8) mm long. Disc florets, 5–19, corolla lobe (0.6–)0.89–1.2–1.4(–1.9) mm long, corolla tube (2.3–)3.4–4.3–5.1(–6.2) mm long; cypselae strigose to densely strigose, (0.8–)1.1–1.6–2.0(–3.3) mm long at anthesis, increasing 2–3 times by maturity, pappus, triple or rarely quadruple: secondary outer series of very few linear scales, 0.1–1mm long; middle and inner series of barbellate bristles, secondary inner series of mid length tapering bristles, 40–75% the length of the primary inner series; primary outer series of tapering bristles 80–95% the length of the primary inner bristles; primary inner series bristles strongly clavate, (3.3–)4.7–5.8–6.8(–8.3) mm long. Chromosomal base number: $x = 9$; all reports diploid ($2n = 18$). Flowering midsummer to early fall.

The pappus has been reported as double in the past (e.g., Cronquist 1980). Hood and Semple (2003) noted that the pappus was biseriate with the outer whorl slightly shorter than the strongly clavate inner whorl with some overlapping of the bases of the bristles. Semple and Hood (submitted) noted that a quadruple pappus was the likely plesiomorphic state in the North American clade; their labels for the four whorls are used here. Further examination of the pappus of *Sericocarpus* species revealed that it is usually triple (Fig. 3). What had been interpreted as a outer whorl of variable length non-clavate bristles is reinterpreted here to be two whorls that sometime grade from the few mid length secondary inner bristles into the primary outer bristles. The secondary inner series bristles tend to be slightly shorter, and thus more distinct, in ray fruit than disc fruit. The primary inner whorl bristles are very obviously clavate and are the longest. Very rarely, a few very short linear scales forming a secondary outer pappus series were present on some fruits; these were not easily

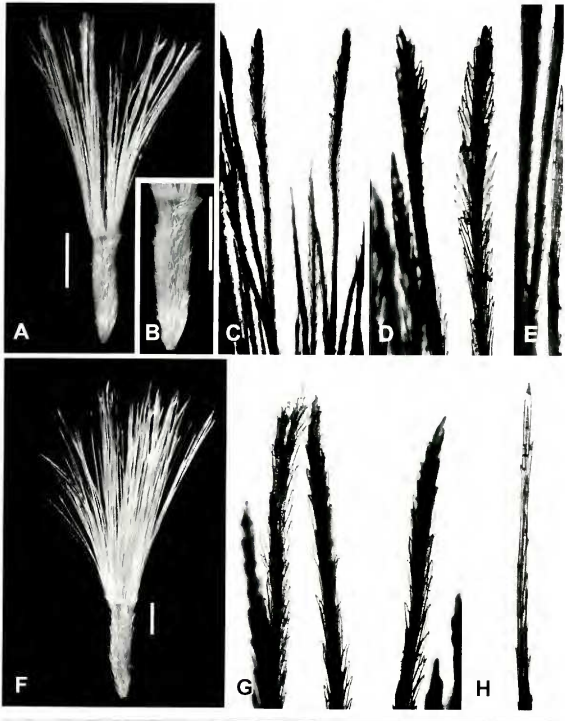

Fig. 3. Fruit traits in *Sericocarpus*, disc fruits; scale bars = 1 mm. **A–F.** *S. asteroides* (*Semple 9566 WAT*). **A.** mature fruit. **B.** Fruit body detail. **C.** Silhouette of upper portion of primary whorls of pappus. **D.** Tips of primary inner whorl bristles. **E.** Tip of secondary inner whorl bristle. **F–H.** *S. tortifolius* (*Semple, Brouillet & Canne 3931* WAT). **F.** Mature fruit. **G.** Tips of primary whorl bristles. **K.** Tips of primary inner whorl bristles. **H.** Tip of secondary outer whorl bristle.

detected and can be obscured by the long hairs of the fruit body. The same rarity occurs in the related genus *Solidago* (Hood and Semple 2003).

KEY TO THE SPECIES OF *SERICOCARPUS*

1. Lower stem leaves dentate, upper leaves becoming entire _____ **2. S. asteroides**
1. All leaves entire
   2. Stems and leaves moderately to densely hispidulous or finely pilose-villous.
      3. Stems hispidulous, hairs 0.1–0.5 mm long; leaves obovate, acuminate to slightly cuspidate, lower leaves < 3 cm in length; phyllaries in 4–5 strongly graduate series _____ **3. S. tortifolius**
      3. Stems hispid-pilose-villous, hairs 0.1–1.5 mm long; leaves elliptical with acute tips, lower leaves > 5 cm in length; phyllaries in 3 series outer half or more the length of the inner _____ **4. S. oregonensis** subsp. **californicus**
   2. Stems and leaves glabrous to sparsely minutely hispidulous.
      4. Leaves linear, involucres 4–6 mm high at anthesis, erect ray florets extending beyond pappus; eastern United States _____ **1. S. linifolius**
      4. Leaves elliptical to (ob)lanceolate, involucres (5–)6–8 mm high at anthesis; erect rays shorter than pappus; California to British Columbia.
         5. Rays 2–5 per head, ray strap >2 mm long _____ **4. S. oregonensis** subsp. **oregonensis**
         5. Rays 1 per head, ray strap <2 mm long _____ **5. S. rigidus**

1. Sericocarpus linifolius (L.) B.S.P., Prel. Cat. N.Y. 26. 1888. non Britt. (1888). (**Fig. 4F**). *Conyza linifolia* L., Sp. Pl. 861. 1753. non *Aster linifolius* L. TYPE: *Kalm s.n.*, Herb. Linn. 993.10, right hand specimen (LINN; LECTOTYPE (Reveal in Jarvis & Turland (ed.), Taxon 47:359. 1998)). Plukenet, Phytographia t. 79, f. 2. 1691 cited in protologue.

Aster solidagineus Michx., Fl. Bor. Amer. 2:108. 1803. *Sericocarpus solidagineus* (Michx.) Nees, Gen. et Sp. Aster. 149. 1832. TYPE: "Hab. in sylvis Carolinae septentrionalis comitatus," *Burke s.n.* (HOLOTYPE: P!). Renaming of *Conyza linifolia* L. Authentic specimens: "Hab. Virginia et Carolina," *Michaux s.n.* (HOLOTYPE: P) *Michaux s.n.* (P!)

Aster solidaginoides Pers., Syn. 2:443. 1807. Orthographic variant of *A. solidagineus* Michx. *Aster solidaginoides* Willd., Sp. Pl. 3:2024. 1803. Orthographic variant of *A. solidagineus* Michx. *Aster solidaginoides* Nees, Syn. Ast. 18. 1818. Orthographic variant of *A. solidagineus* Michx.

Perennial herb from stout, branching, woody caudex. Stem erect, glabrate, (22–)34–47–60(–75) cm, striate, the narrow membranous ridges often reddish. Basal leaves absent at time of flowering. Stem leaves, linear, sessile, acuminate, (1–)2–4–5(–8) cm long, (0.1–)0.2–0.4–0.6(–1) cm wide, reticulate veined, glabrate, glandular punctuate, margins ciliate, entire, upper leaves decreasing in size upward. Capitulescence broadly corymbiform; heads 2–4 per branch; bracts, ciliate, glabrate, broadly lanceolate to narrowly ovate. Involucre (3.8–)4.2–4.6–5.0(–5.5) mm high at anthesis, (2.3–)2.5–3.2–3.9(–4.8) mm wide; phyllaries in 3–4 imbricate series, glabrate, base widely oblong, tip broadly acute, outer series (2.4–)2.7–3.0–3.2(–3.5) mm long, mid series (3.0–)3.3–3.6–4.0(–4.4) mm long, inner series more linear and less chlorophyllous, margins ciliate, dark chlorophyll zone at the apex, thumb-nail shaped. Ray florets, 2–6, strap (4.2–)4.5–6.0–7.5(–10.5) mm long, corolla tube (2.4–)2.7–3.1–3.5(–4.0) mm long, cypselae densely strigose, (0.7–)0.8–1.0–1.1(–1.2) mm long at anthesis, increasing twofold by maturity,

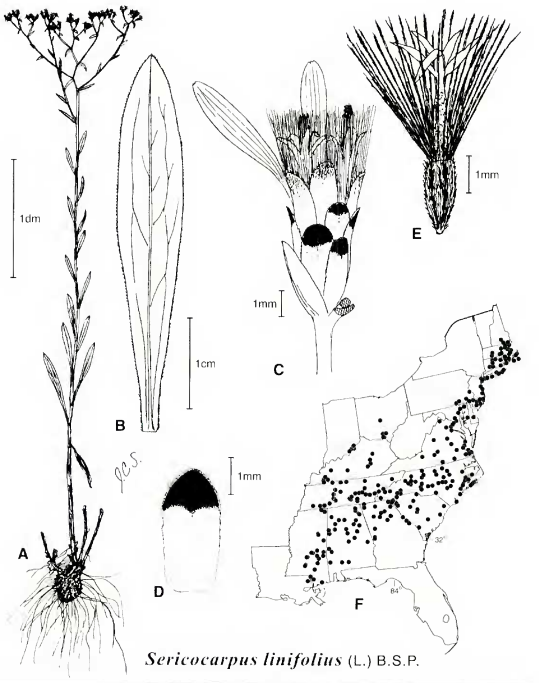

Fig. 4. Morphology and distribution of *Sericocarpus linifolius*. **A.** Habit. **B.** Lower mid stem leaf. **C.** Head, on only some florets shown; hatch marks indicated location of bract and second head (not shown). **D.** Mid series phyllary with chlorophyllous zone dark. **E.** Mature disc floret achene with floret still attached. **F.** Distribution in the eastern United States based on all collections seen.

pappus double or rarely quadruple; secondary outer linear scales 0–very few, 0.1–1mm long; secondary inner bristles few, 40–60% of primary inner series; primary outer bristles 70–90% of inner bristles; primary inner bristles moderately strongly clavate, (3.5–)3.9–4.3–4.7(–5.1) mm long. Disc florets, 5–15, corolla

lobe (1.1–)1.2–1.5–1.7(–1.9) mm long, corolla tube (2.3–)2.7–3.1–3.5(–3.8) mm long; cypselae densely strigose, (0.8–)0.9–1.0–1.1(–1.3) mm long at anthesis, increasing 2 fold by maturity; pappus triple or rarely quadruple: secondary outer linear scales 0–very few, 0.1–1mm long; secondary inner bristles few, 40–60% of primary inner series; primary outer bristles 70–90% of inner bristles; primary inner bristles strongly clavate, (3.3–)4.1–4.5–5.0(–5.5) mm long. Chromosome number: $2n = 18$.

Flowering midsummer–early fall. Dry to moist sandy, clay and gravelly open soils of open deciduous and pine woods, oak and pine barrens, roadsides, fields; 5–850 m; southern New Hampshire, Massachusetts, Rhode Island, Connecticut, New Jersey, Long Island and adjacent New York, southeastern Pennsylvania, eastern Maryland, Delaware, D.C., Virginia, West Virginia, Kentucky, into southern Ohio and extreme southeastern Indiana, North Carolina, Tennessee, South Carolina, northern Georgia, Alabama, Mississippi, and extreme eastern Louisiana.

2. Sericocarpus asteroides (L.) Nees, Gen. et Sp. Aster. 150. 1832. (**Figs. 3A–E, 5**)

Conyza asteroides L., Sp. Pl. 2:861. 1753. *Sericocarpus asteroides* (L.) B.S.P., Prel. Cat. N.Y. 26. 1888. *Aster asteroides* (L.) MacMillan, Meta. Minn. 524. 1892. TYPE: Herb. Linn. 993.10, the two left-hand specimens (LINN!; LECTOTYPE: [Reveal et al., Huntia 7:214. 1987]).

Aster conyzoides Willd., Sp. Pl. 3:2043. 1803, non Desf. (1829). Substitute name for and typified by *Conyza asteroides* L.

Aster marylandicus Michx., Fl. Bor. Amer. 2:108. 1803. Based illegitimately on *Conyza asteroides* L. (see Cronquist (1947) for discussion).

Sericocarpus conyzoides (L.) Nees *_plantaginifolius* Nees, Gen. et Sp. Aster. 150. 1832. TYPE: U.S.A. NEW JERSEY: *Nuttall s.n.* (HOLOTYPE: not seen).

Sericocarpus asteroides (L.) B.S.P. f. *albopapposus* Farwell, Pap. Michigan Acad. Sci. 1:100. 1923. TYPE: U.S.A. MICHIGAN: Galesburg, 31 Aug 1818, *Farwell 5097a* (HOLOTYPE: not seen).

Sericocarpus asteroides (L.) B.S.P. f. *roseus* H.K. Svenson, Rhodora 30:136. 1928. TYPE: U.S.A. MASSACHUSETTS: Falmouth, "in sandy soil," 1 Sep 1926, *Svenson s.n.* (HOLOTYPE: GH!)

Aster paternus Cronq., Bull. Torrey Bot. Club 74:149. 1947. Based on *Conyza asteroides* L.

Perennial herb from short-branching woody caudex. Stem very sparsely to moderately hispidulous-puberulent, erect, (14–)26–39–52(–65) cm. Basal leaves present at time of flowering, (2–)4–8–11(–15) cm long, serrate near apex, spatulate to petiolate, reticulate veined, puberulent. Stem leaves, narrowly to broadly ovate, sessile, (1–)2–4.0–6(–11) cm long, (0.4–)0.6–1–2(–3) cm wide, cuneate, acuminate to acute, reticulate veined, glabrate to sparsely hispidulous, sparsely to moderately glandular punctuate, margins ciliate, serrate, upper leaves decreasing in size upward, becoming entire. Capitulescence corymbiform; heads 2–5 per branch. Involucre (4.2–)5.0–5.7–6.4(–7.1) mm high at anthesis, (3.1–)3.8–4.4–5.1(–6.0) mm wide; phyllaries in 3–4 imbricate series, broadly lanceolate to narrowly ovate, outer series (2.4–)2.8–3.3–3.7(–4.2) mm long, mid series (3.3–)3.9–4.4–5.0(–5.4) mm long, inner more linear and less chlorophyllous, margins ciliate, dark chlorophyll zone at the apex, thumb-nail shaped. Ray florets, 3–7,

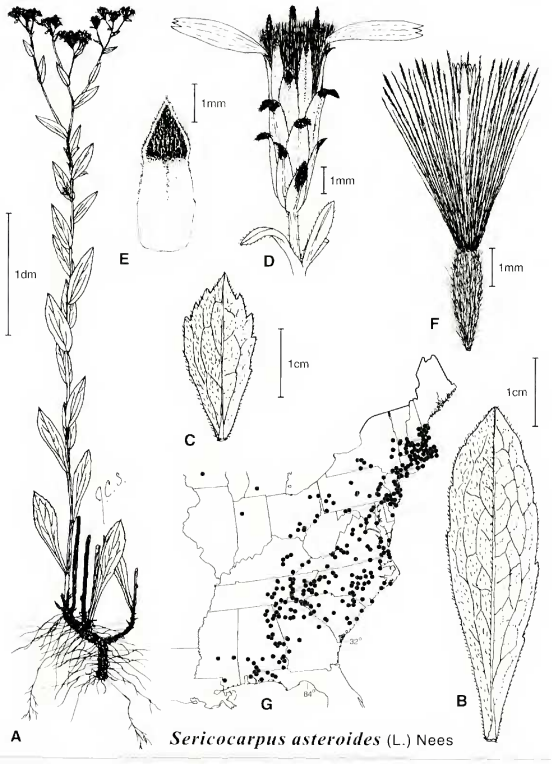

Fig. 5. Morphology and distribution of *Sericocarpus asteroides*. **A.** Habit. **B.** Lower mid stem leaf. **C.** Small serrate leaf. **D.** Head, on only some florets shown. **E.** Mid series phyllary with chlorophyllous zone dark. **F.** Mature disc floret achene with floret still attached. **G.** Distribution in the eastern United States based on all collections seen; the collections from Michigan is based on a literature report and was not seen.

strap (2.5–)3.5–4.3–5.2(–6.0) mm long, corolla tube (2.4–)2.6–3.1–3.5(–4.2) long, cypselae, densely strigose, (0.8–)1.0–1.2–1.4(–1.8) mm long at anthesis, increasing twofold by maturity, pappus triple or rarely quadruple: secondary outer linear scales 0–very few, 0.1–1mm long; secondary inner bristles few, 40–75% of primary inner series; primary outer bristles 70–90% of inner bristles; primary inner bristles moderately strongly clavate, (3.6–)4.0–4.4–4.8(–5.2) mm long. Disc florets, 9–20, corolla lobe (0.6–)0.8–0.9–1.1(–1.5) mm long, corolla tube (3.2–)3.4–3.7–4.0(–4.4) mm long; cypselae densely strigose, (0.8–)1.1–1.3–1.5(–1.7) mm long at anthesis, increasing twofold by maturity, pappus triple or rarely quadruple: secondary outer linear scales 0–very few, 0.1–1mm long; secondary inner bristles few, 50–70% of primary inner series; primary outer bristles 70–90% of inner bristles; primary inner bristles strongly clavate, (3.7–)4.3–4.7–5.0(–5.4) mm long. $2n = 18$.

Flowering mid summer to early fall. Dry sandy, clay, and shaly open soils in fields and open mixed and pine woods, road margins; 3–1550 m; extreme southern Maine, New Hampshire, Vermont, Massachusetts, Rhode Island, Connecticut, New Jersey, New York, Pennsylvania, Ohio, Maryland, Delaware, D.C., Virginia, West Virginia, eastern Kentucky, North Carolina, eastern Tennessee, South Carolina, northern and central Georgia, Alabama, and southern Mississippi (Fig. 5G). The species has not been reported from Louisiana (Gandhi and Thomas 1989; USDA, plants.usda.gov web site). Single collections of *S. asteroides* labeled as being from northwestern Indiana and south central Wisconsin are of questionable provenance or are likely chance introductions. A single collection reported from southwestern Michigan was not seen; this also is most likely an introduction or of "dubious status" (Voss 1996).

3. Sericocarpus tortifolius (Michx.) Nees, Gen. et Sp. Aster. 151. 1832. (**Figs. 3F–H, 6**) *Aster tortifolius* Michx., Fl. Bor. Amer. 2:109. 1803. non (Torr. & A. Gray) A. Gray (1868). TYPE: U.S.A. "Hab. in Carolina inferiore," *Michaux s.n.* (HOLOTYPE: P-MICHX!; ISOTYPE: P, several pieces on one sheet).

Conyza bifoliata Walt., Fl. Car. 204. 1788. non L. (1753), non Cham. & Less. (1831). *Sericocarpus bifoliatus* (Walt.) Porter, Mem. Torrey Bot. Club 5:322. 1894. *Aster bifoliatus* (Walt.) Ahles, J. Elisha Mitchell Sci. Soc. 80:173. 1964. TYPE: U.S.A. Carolinas? (HOLOTYPE/LECTOTYPE: BM?, not seen, not on p.36 of Schubert's photographs of Walter Herbarium)

Sericocarpus collinsii Nutt., Trans. Am. Phil. Soc. 2, 7:302. 1841. *Sericocarpus bifoliatus* (Walt.) Porter var. *collinsii* (Nutt.) Blake, Proc. Amer. Acad. Arts 51:515. 1916. TYPE: U.S.A. EAST FLORIDA: Mr. Ware (HOLOTYPE: BM, not seen; simple sketch seen) ¡

Sericocarpus acutisquamus Small, Fl. S.E.U.S. 1206, 1339. 1903. TYPE: U.S.A. FLORIDA. Columbia Co.: Lake City, 29–31 Aug 1895, *G.V. Nash 2486* (HOLOTYPE: NY ex Columbia College!). Small lists *Sericocarpus bifoliatus* (Walt.) Porter var. *acutisquamus* Nash but this name does not appear to have been published.

Perennial herb from short-branching woody caudex. Stem erect, (33–)39–61–83(–117) cm, puberulent, hispidulous-pilose-villous hairs 0.1–0.5 mm long, sparsely stipitate-glandular. Basal leaves absent at time of flowering. Stem leaves sessile, obovate, acuminate to slightly cuspidate, (0.9–)1–2–3(–4) cm long, (0.3–)

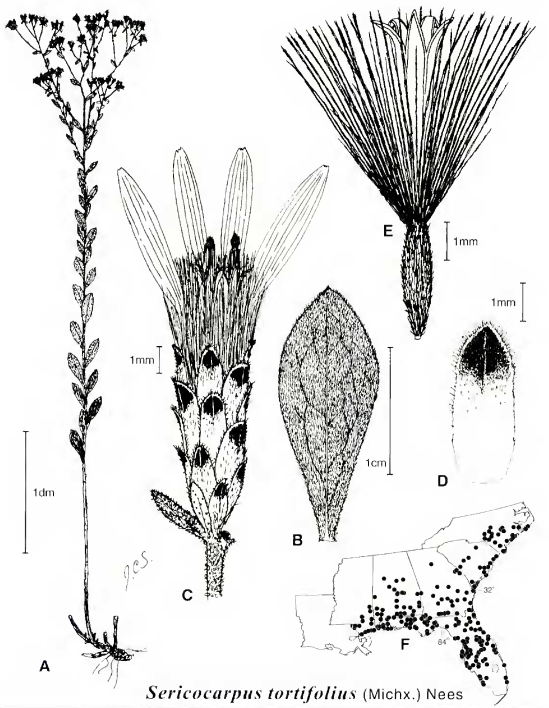

Fig. 6. Morphology and distribution of *Sericocarpus tortifolius*. **A.** Habit. **B.** Lower mid stem leaf. **C.** Head, only some florets shown. **D.** Mid series phyllary with chlorophyllous zone dark. **E.** Mature disc floret achene with floret still attached. **F.** Distribution in the eastern United States based on all collections seen.

0.6–0.8–1(–1) cm wide, reticulate veined, sparsely to moderately finely pilose-scabrous, hairs 0.05–0.1 mm long, finely glandular punctuate, the stipitate glands minute, margins ciliate, entire, upper leaves decreasing in size upward. Capitulescence corymbiform, heads 2–4 per branch; bracts, ciliate, pubescent, broadly lanceolate to narrowly ovate. Involucre (4.8–)5.2–6.0–6.7(–8.0) mm high

at anthesis, (3.1–)3.8–4.4–5.1(–6.0) mm wide; phyllaries in 4–5 imbricate series, ciliate, puberulent base widely oblong, tip acute, outer series (1.8–)1.9–2.2–2.6 (–3.1) mm long, first mid series (2.7–)2.8–3.2–3.7(–4.4) mm long, second mid series (3.6–)3.9–4.4–5.0(–6.1), inner series more linear and less chlorophyllous, margins ciliate, dark chlorophyll zone at the apex, thumb-nail shaped. Ray florets, 2–5, strap (3.4–)3.9–4.8–5.7(–6.4) mm long, corolla tube (2.7–)3.0–3.4–3.8(–4.2) long, cypselae densely strigose, (1.1–)1.2–1.5–1.8(–2.4) mm long at anthesis, increasing twofold by maturity, pappus triple or rarely quadruple: secondary outer linear scales 0–very few, 0.1–1mm long; secondary inner bristles few, 40–70% of primary inner series; primary outer bristles 80–90% of inner bristles; primary inner bristles moderately strongly clavate, (5.4–)5.9–6.5–7.1(–7.8) mm long. Disc florets, 6–11, corolla lobe (1.1–)1.2–1.4–1.6(–1.8) mm long, corolla tube (3.8–)4.19–4.82–5.5(–5.6) mm long; cypselae densely strigose, (1.2–)1.2–1.5–1.9(–2.6) mm long at anthesis, increasing twofold by maturity, pappus triple or rarely quadruple: secondary outer linear scales 0–very few, 0.1–1mm long; secondary inner bristles few, 50–70% of primary inner series; primary outer bristles 80–90% of inner bristles; primary inner bristles moderately strongly clavate, (5.7–)6.2–6.8–7.4(–8.3) mm long. $2n = 18$.

Flowering midsummer–early fall. Dry to moist clay, sandy and gravelly open soils in oak and pine barrens, oak scrub, pastures, roadsides, mostly coastal plain; ca. 5–200 m; eastern North Carolina, South Carolina, Georgia, Florida, Alabama, southeastern Mississippi and adjacent Louisiana.

4. Sericocarpus oregonensis Nutt., Trans. Amer. Phil. Soc. 2, 7:302. 1840. (**Fig. 7**)
Aster oregonensis (Nutt.) Cronq., Vasc. Fl. Pacif. Northw. 5:91. 1955. "Round Ft. Vancouver" [protologue]. "Margins of Wahlament & Wappatoo Island" [Nuttall's handwritten label], 1835?, *Nuttall s.n.* (HOLOTYPE: BM, photo!).

Perennial herb from stout, branching, woody caudex. Stem erect, (24–)40–62–85(–102) cm, glabrous to very sparsely hispidulous-scabrous, hairs 0.05 mm long, or moderately to densely hispidulous-pilose-villous, hairs 0.1–1.5 mm long, sometimes resinous-glandular. Basal leaves absent at time of flowering. Stem leaves broadly lanceolate to narrowly ovate, sessile, acuminate to acute, (1–)2–4–6(–10) cm long, (0.3–)0.6–0.9–1(–2) cm wide, reticulate veined, finely scabrous or hispidulous-scabrous, more densely so on the abaxial veins, the hairs 0.1–0.5(–2) mm long, glandular punctuate to very resinous, margins ciliate, entire, upper leaves decreasing in size upward. Capitulescence corymbiform; heads 2–4 per branch; bracts, ciliate, pubescent, broadly lanceolate to narrowly ovate. Involucre (4.7–)5.7–6.4–7.0(–7.2) mm high at anthesis, (4.4–)5.0–5.8–6.6(–7.2) mm wide; phyllaries in 3–4 imbricate series, ciliate, puberulent, base narrowly oblong, acuminate, outer series (2.8–)3.4–3.9–4.4(–4.6) mm long, mid series (3.8–)4.5–5.0–5.4(–5.6) mm long, inner series more linear and less chlorophyllous, margins ciliate, dark chlorophyll zone at the apex, thumb-nail shaped. Ray florets,

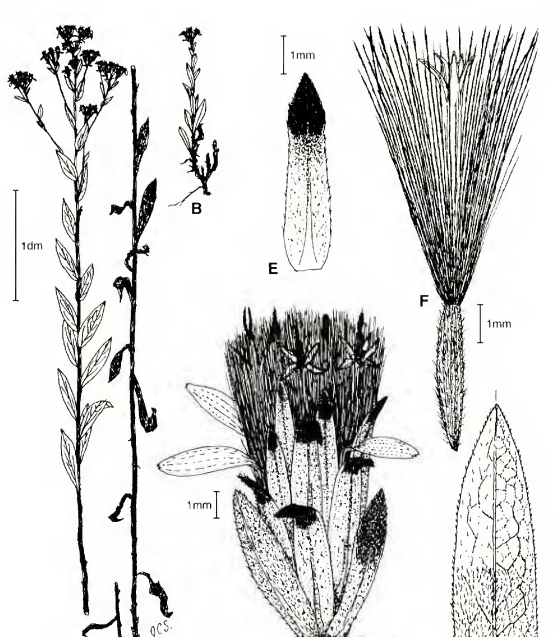

FIG. 7. Morphology of *Sericocarpus oregonensis*. **A–B.** Habits of large and small plants, respectively. **C.** Lower mid stem leaf; upper half subsp. *oregonensis*, lower half subsp. *californicus*. **D.** Head, on some florets shown; hatch marks indicated location of bract and second head (not shown). **E.** Mid series phyllary with chlorophyllous zone dark. **F.** Mature disc floret achene with floret still attached.

2–6, strap (3.1–)3.7–4.5–5.2(–5.6) mm long, corolla tube (2.6–)2.8–3.2–3.5(–3.8) mm long, cypselae strigose, (1.3–)1.5–2.1–2.6(–3.3) mm long at anthesis, increasing two–threefold by maturity, pappus triple or rarely quadruple: secondary outer linear scales 0–very few, 0.1–1mm long; secondary inner bristles few, 40–75% of primary inner series; primary outer bristles 80–95% of inner bristles; primary inner bristles moderately strongly clavate, (4.1–)4.7–5.3–5.9(–6.6) mm long. Disc florets, 9–20, corolla lobe (1.0–)1.1–1.2–1.4(–1.7) mm long, corolla tube (3.4–)4.1–4.6–5.1(–5.2) mm long; cypselae strigose, (1.4–)1.7–2.2–2.7(–3.3) mm long at anthesis, increasing twofold by maturity, pappus triple or rarely quadruple: secondary outer linear scales 0–very few, 0.1–1mm long; secondary inner bristles few, 40–75% of primary inner series; primary outer bristles 80–95% of inner bristles; primary inner bristles moderately strongly clavate, (4.8–)5.5–6.1–6.7(–7.2) mm long. $2n = 18$.

4a. Sericocarpus oregonensis subsp. **oregonensis (Figs. 7c, 8).** *Sericocarpus oregonensis* var. *oregonensis*. *Aster oregonensis* subsp. *oregonensis*.

Flowering midsummer to early fall. Stems glabrous-glabrate, the hairs minutely scabrous; leaves glabrous to very sparsely and minutely hispidulous-pilose, hairs 0.05 mm long, obviously resinous especially along the veins. Dry to moist sandy to rocky soils in open areas in oak and pine woods, brushlands, roadsides, disturbed habitats; 100–1800 m; Coast and Cascade ranges, Washington where it is rare, western Oregon, and northern California south to Mendocino County.

4b. Sericocarpus oregonensis Nutt. subsp. **californicus** (Durand) Ferris, Contr. Dudley Herb. 5:100. 1958. (**Figs. 7c, 8**). *Sericocarpus californicus* Durand, J. Acad. Nat. Sci. Phil. 2, 390. 1855. non *Aster californicus* Less. in Schldl. & Cham. (1831), nec Kuntze (1891). *Sericocarpus rigidus* Lindl. in Hook. var. *californicus* (Durand) Blake, Proc. Amer. Acad. Arts 51:515. 1916. *Aster oregonensis* (Nutt.) Cronq. subsp. *californicus* (Durand) Keck., Aliso 4:105. 1958. TYPE: U.S.A. CALIFORNIA. Nevada Co.: Nevada City, *Rattan* s.n. (HOLOTYPE: P, fragment NY)

Flowering midsummer–early fall. Stems moderately to densely hispidulous-pilose, the longest hairs villous twisted, hairs 0.1–1.5 mm long; leaves moderately hispidulous-scabrous, more densely so along the abaxial veins, the hairs on the surface 0.1–0.5 mm long, those on the veins to 1–2 mm long, finely glandular punctate. Dry to moist sandy soils in open areas in oak and pine woods, along dry streams, granitic and serpentine barrens; 800–2200 m; Sierra Nevada Range of eastern California.

5. Sericocarpus rigidus Lindl. in Hook., Fl. Bor.-Amer. 2:14. 1834. (**Fig. 9**). SYNTYPES: U.S.A. OREGON or WASHINGTON: Columbia River, *Scouler* s.n. (LECTOTYPE [Cronquist 1955]: CGE?, not found in search of types; ISOLECTOTYPE: NY ex Torrey!).

Sericocarpus rigidus Lindl. in Hook. var. *laevicaulus* Nutt., Trans. Amer. Phil. Soc. 2, 7:302. 1840. TYPE: U.S.A. WASHINGTON. Fort Vancouver, *Nuttall* s.n. (HOLOTYPE: not seen)

Aster curtus Cronquist, Vasc. Fl. Pacif. Northw. 5:80. 1955. New name for *Sericocarpus rigidus* Lindl. in Hook. (1834).

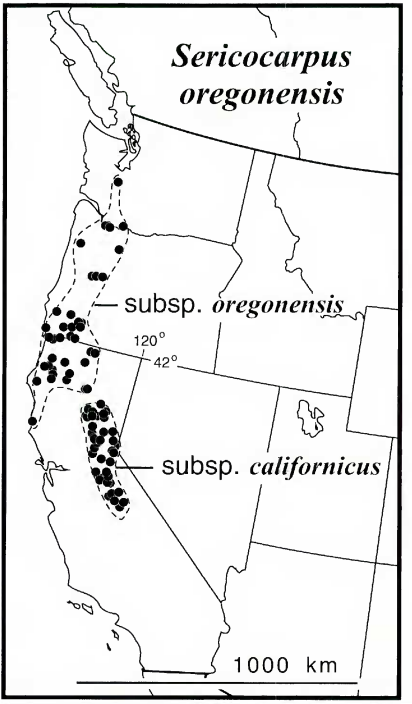

Fig. 8. Distribution of *Sericocarpus oregonensis* in the western United States based on all collections seen.

Perennial herb from short, branching, rhizomatous, woody caudex. Stem erect, puberulent, (19–)21–28–34(–37) cm. Basal leaves absent at time of flowering. Stem leaves, puberulent, obovate, sessile, acute, upper leaves becoming acuminate, (1–)2–3–4(–6) cm long, (0.3–)0.5–0.6–0.8(–0.9) cm wide, reticulate veined, margins ciliate, entire, upper leaves decreasing in size upward. Capitulescence broadly corymbiform, compact; heads 2–3 per branch; bracts ovate, ciliate,

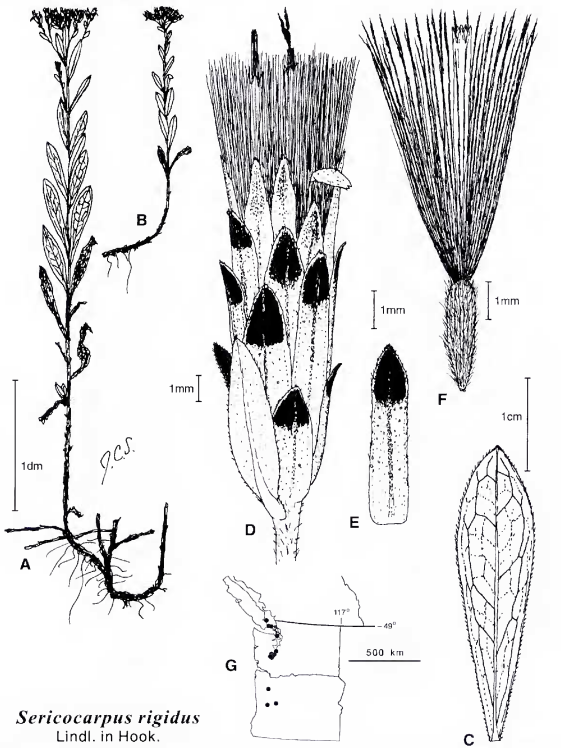

FIG. 9. Morphology and distribution of *Sericocarpus rigidus*. **A–B.** Habits or large and small plants, respectively. **C.** Mid stem leaf. **D.** Head, only some florets shown. **E.** Mid series phyllary with chlorophyllous zone dark. **F.** Mature disc floret achene with floret still attached. **G.** Distribution in the Oregon, Washington and British Columbia based on all collections seen.

puberulent. Involucre (6.1–)6.4–7.3–8.1(–8.6) mm high at anthesis, (4.1–)4.7–5.6–6.4(–6.5) mm wide; phyllaries in 3–4 imbricate series, slightly ciliate, puberulent, base narrowly oblong, tip acuminate to acute, outer series (3.1–)3.5–4.2–4.9(–5.3) mm long, mid series (4.6–)4.7–5.5–6.2(–6.5) mm long, inner series more linear and less chlorophyllous, margins ciliate, dark chlorophyll zone at the apex, thumb-nail shaped. Ray florets, 1–2, strap, ligulate, (1.6–)1.6–2.1–2.6(–3.0) mm long, corolla tube (2.5–)2.6–3.1–3.5(–3.9) mm long, cypselae strigose, (1.3–)1.2–1.6–1.9(–2.2) mm long at anthesis, increasing twofold by maturity pappus triple or rarely quadruple: secondary outer linear scales 0–very few, 0.1–1mm long; secondary inner bristles few, 40–75% of primary inner series; primary outer bristles 80–95% of inner bristles; primary inner bristles moderately strongly clavate, (4.6–)5.1–5.7–6.2(–6.5) mm long. Disc florets, 9–17, corolla lobe (0.6–)0.7–0.8–0.9(–1.0) mm long, corolla tube (4.4–)4.6–5.1–5.6(–6.2) mm long; cypselae strigose, (1.4–)1.5–1.8–2.1(–2.3) mm long at anthesis, increasing twofold by maturity, pappus triple or rarely quadruple: secondary outer linear scales 0–very few, 0.1–1mm long; secondary inner bristles few, 40–75% of primary inner series; primary outer bristles 85–95% of inner bristles; primary inner bristles moderately strongly clavate, (5.7–)6.2–6.6–7.1(–7.4) mm long, $2n = 18$.

Flowering midsummer to early fall. Prairie habitats, dry pastures, dry grassy Garry oak forests with rocky outcrops; 10–120 m; extreme southern British Columbia, western Washington, and scattered disjunct locations in western Oregon (Fig. 6G). *Scricocarpus rigidus* grows on the southern part of Vancouver Island, B.C. and in scattered locations to the south end of the Puget Sound area in Washington. The species is rare throughout its range and is listed by COSEWIC in Canada as Threatened, by USFWS as Species of Concern, as Sensitive in Washington, and as Threatened in Oregon.

ACKNOWLEDGMENTS

This research was supported by Natural Sciences and Engineering Research Council of Canada Operating and Discovery Grants to J.C.S., a Natural Sciences and Engineering Research Council of Canada Post Graduate Scholarship and an Ontario Graduate Scholarship to R.E.C. This work was initiated as a Biol499 Senior Research Project at University of Waterloo by M.R.L. Gina Murrell (CGE) is thanked for assistance in attempts to locate type material of *S. rigidus* in 2004. Guy Nesom and David Keil are thanked for their helpful suggestions in their reviews of the manuscript.

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